MORPHOLOGICAL VARIATION OF ELODEA IN WESTERN MASSACHUSETTS: FIELD AND LABORATORY STUDIES

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The genus *Elodea* Michaux (Helobiae: Hydrocharitaceae) consists of 17 species, nine of which are distributed in North America and eight in South America. In North America *E. canadensis* Rich. in Michx. is the most widespread species, spanning the continent from Quebec to British Columbia, south to Alabama and California. *Elodea nuttallii* Planch. has the second widest range, occurring abundantly from the lowlands in Maine to North Carolina, west to Missouri, and also in Idaho. Other North American species are extremely restricted in range or are known only from single localities. Neither *E. canadensis* nor *E. nuttallii* has been reported in South America (St. John, 1965).

Elodea canadensis and *Elodea nuttallii* are economically important plants because of their frequent occurrence as troublesome waterweeds. Studies indicate that these two species are present at different stages in the eutrophication of a lake and that *E. nuttallii* may have a greater tolerance to various forms of pollution, including nutrient enrichment, than *E. canadensis* (Stuckey, 1971; Lind and Cottam, 1969; Volker and Smith, 1965).

Plants of both *Elodea canadensis* and *E. nuttallii* are dioecious. The flowers of the two species differ primarily in size. Those of *E. canadensis* are larger, and at flowering both the staminate and pistillate flower buds are raised by filiform hypanthia to the water's surface where anthesis and pollination take place. Pistillate flowers of *E. nuttallii* are also raised by elongation of the hypanthium, but staminate flowers of this species are sessile. Just prior to anthesis the staminate flowers abscise and float to the surface of the water, where they open. Their pollen is shed on the surface of the water and floats to the pistillate flowers (St. John, 1965).

Pollination and seed formation are extremely rare. Reasons for this are the brief and infrequent flowering periods and the differing abundance of the two sexes in nature, pistillate plants being collected much more often than staminate plants. At nearly every locality of staminate plants, pistillate plants are known to occur also, although the reverse is not true.

A distinction has often been made between pistillate and staminate plants of *Elodea canadensis* to the extent that the staminate plants were at one time believed to represent a separate species. Staminate flowers differ from pistillate ones in having longer sepals and petals. The leaves of successive nodes on the holotype and on most of the staminate plants which St. John examined (1965) were more widely spaced, narrower, and thinner than those of pistillate plants. However, in some collections of flowering staminate plants, the broad, firm, imbricate leaves were indistinguishable from those of pistillate plants (St. John, 1965). The distinction between male and female plants on the basis of vegetative morphology alone is, therefore, neither valid nor dependable.

Due to the brief flowering period, the minute size of the flowers and infrequent flowering, leaf size, shape, and arrangement are often the only criteria available to differentiate species. The vegetative phase of *Elodea* is submerged, and both *E. canadensis* and *E. nuttallii* grow either rooted in the bottom or free-floating. Plants of *Elodea canadensis* have a firm, dark green appearance, with ovate to oblong leaves crowded and densely imbricated near the apex. *Elodea nuttallii* plants are slenderer, pale green, and flaccid, with linear or narrowly linear lanceolate leaves. Table 1 gives ranges and some averages of leaf widths of *E. canadensis* and *E. nuttallii* published in recent treatments. Leaf length of both species is in the range of 6-17 mm (Fernald, 1950).

Problems of misidentification of species of *Elodea*, particularly *E. canadensis* and *E. nuttallii*, appear to be compounded by phenotypic plasticity in the vegetative or-

ans of the plant. Additionally, the superficial similarity of he vegetative state of *Egeria densa* Planch. (once treated s *Elodea canadensis* var. *gigantea;* see St. John, 1965, and Marie-Victorin, 1931) to that of *Elodea* spp. has introuced errors in reports of chromosome counts, habit descriptions and range delineations due to misdeterminations.

Vegetative reproduction in both species is the primary neans of regeneration. The brittle and delicate stems are asily fragmented by currents, winds, motorboat traffic, oraging animals, or other disturbance. Any part of the xis is capable of producing a new plant if a dormant ateral bud is present and the fragment does not become lesiccated (Sculthorpe, 1967). Fragments can become ooted in new locations by means of adventitious roots roduced at the nodes.

Reductions of leaf width in *Elodea canadensis* in reponse to nutrient enrichment have been reported (Adams t al., 1971). Preliminary observations of the vegetative growth of *E. canadensis* and *E. nuttallii* raised in tanks

TABLE 1

Ranges and averages of leaf widths of *Elodea canadensis* nd *Elodea nuttallii* in recent treatments.

Author	*E. canadensis*	*E. nuttallii*
Fernald (1950)	1.0-5.0 mm	0.3-1.5 mm
St. John (1965)	1.0-5.0 mm	0.3-1.5 mm
Livingston (1967)	2.0-5.0 mm	1.2-1.5 mm
Seymour (1969)	1.0-5.0 mm	0.3-1.5 mm
Radford et al. (1964)	1.0-5.0 av. 2.0 mm	$\leq$ 1.5 av. 0.3 mm
Gleason (1952)	1.2-4.0 av. 2.0 mm	0.7-1.8 av. 1.3 mm
Wassett (1969)	1.2-4.5 av. 2.0 mm	0.7-1.8 av. 1.3 mm
Muenscher (1944)	1.2-4.0 av. 2.0 mm	0.7-1.8 av. 1.3 mm

at higher temperatures than normally encountered in t
field revealed morphological variation in *E. canadens*
An experiment was therefore devised to determine t
extent of this morphological change in vegetative plan
induced by growing specimens at various temperatur
The study also attempted to determine whether accept
taxonomic criteria for distinguishing *E. canadensis* a
E. nuttallii are effective in natural populations.

Effects of Elevated Temperature on the Vegetative Morphology of Elodea canadensis

Materials and Methods

Plants of *Elodea canadensis* were collected from Bro
Brook near its entry into Nashawannuck Pond, Eastham
ton, Massachusetts. Water temperatures in Broad Broo
which is fed in part by natural artesian wells, were mea
ured at biweekly intervals during summer, 1973, at t
collection site. Mean temperature in Broad Brook w
13.5 C. No readings deviated more than one degree Cen
grade from the mean. Plants were removed from t
collecting site at the substrate level, placed in gallon ja
filled with pond water for transport to the Lyman Pla
House at Smith College, briefly rinsed with tap wate
and cut to 8 cm lengths. Each 8 cm piece had a growi
tip and was without branches or roots.

Eight 5.7 liter (6 qt.), all glass, rectangular aquar
were used for culture. Sand 4-6 cm deep was placed
each tank, and the tanks were filled with water fro
Broad Brook. Twenty-five 8 cm plants were placed in ea
tank with the lower portions of the stem embedded in t
sand. The tanks were marked and placed in a water ba
with non-transparent sides which shaded them so that, f
the most part, plants received light only through the su
face of the water.

All growth experiments were conducted in the Lyman Plant House, where plants received natural day lengths and were subject to day-night and day-to-day temperature fluctuations. Water lost through evaporation was replaced. Daytime temperatures ranged from 19 C to 30 C with a mean of 25.6 C.

Plants were harvested, measured, and pressed at intervals of 1 week, 2 weeks, 4 weeks, 5 weeks, and 7 weeks. Fifteen plants were measured each time except week 5, when by error six were measured. Since the measuring process destroyed the plants, five additional specimens were pressed and reserved as vouchers each week. These were deposited in the herbarium of Smith College. Parameters measured were length, weight, whorls/2 cm, width of leaves, and length of leaves. Ten leaves were removed from each plant and measured with a millimeter ruler. On plants 1 week old, the first five leaves measured were from the area of the original 8 cm of the plant. The rest were spaced evenly up the newly grown portion of the stem. In following weeks, the procedure was the same except only three of the leaves measured were from the original section of the plant. The experiment began July 2, 1973, and the final measurements were taken August 20, 1973.

DISCUSSION

The number of leaves having widths less than or equal to 1.5 mm increased on cultured specimens of *Elodea canadensis* as the experiment progressed (Table 2). Regression analysis (Sokal and Rohlf, 1969) of the relationship between number of leaves 1.5 mm or less in width and age in weeks reveals a highly significant positive regression ($.02 > P > .01$).

Plants grown in Broad Brook under field conditions at an average temperature of 13.5 C represent the control group. These specimens of *Elodea canadensis* did not show a change in leaf size. Mean width of leaves was 2.62 mm with a range of 2.0-4.0 mm.

Leaves produced in culture tended to resemble *Elodea nuttallii*. This effect was more pronounced during later phases of the experiment. Leaves on the original 8 cm of each plant retained their initial dimensions (3-4 mm). Leaves produced above them were narrower (2-3 mm), and this area of intermediate-sized leaves was followed by a portion of stem having very short, narrow leaves (1.75-2.25 mm). All growth above that section consisted of longer, more narrow leaves (1.25-1.75 mm). Leaves produced in culture were paler green and more flaccid than those present at the beginning of the experiment.

Morphological Variation in Selected Populations of Elodea in Western Massachusetts

MATERIALS AND METHODS

Elodea plants were sampled at 20 localities throughout western Massachusetts. Publications No. 10-2 (McCann and Daly, undated), No. 10-4 (McCann and Daly, 1972), and No. 11 (Livingston and Bentley, undated) of the Water Resources Research Center at the University of Massachusetts were used as guides to the location of possible collection sites.

A single measurement of water temperature was made at each site. Temperatures varied from 13 C at Broad Brook to 33 C at Buck Pond. At 11 sites, water temperatures were 25 C or higher at the time of collection.

Collected plants were placed in labeled jars with pond water. Plants were rinsed, cut into 8 cm pieces, and weighed. The number of whorls per 2 cm length, and the length and width of five leaves on each of 20 plants were measured in all but three populations in which only ten plants were available for measurement.

Collections were made from July 3 to September 16, 1973.

TABLE 2

Percent of total number of leaves measured which had a width < 1.5 mm on specimens of *Elodea canadensis* at times before and during culture.

Weeks in Culture	Percent of leaves < 1.5 mm
0	0
1	3.3
2	19.3
4	28.0
5	30.0
7	37.3

DISCUSSION

All plants collected occurred in water not more than 1.5 meters deep. Characteristic habitats were silt, sand on silt, and sand substrates in water of slow to moderate current velocity. Lakes where *Elodea* was found had open water, were heavily used by man in most cases, and had moderate aquatic vegetation cover. Isolated lakes with little submergent vegetation, rocky bottoms, and limited use did not support *Elodea*, nor did highly eutrophic lakes with little open water and thick covers of *Nymphaea odorata*, *Nuphar variegatum*, *Pontederia cordata*, and *Lemna minor*. Sites where plants were collected varied from clean, clear water to polluted, turbid conditions.

Leaf length of *Elodea canadensis* and *E. nuttallii* are generally described as similar (St. John, 1965; Fernald, 1950); hence only leaf width was used to differentiate species. Table 3 is a list of the collection sites, their location by town, and the range, 95% confidence interval, and mean of the leaf width of each population. Two level nested anova (Sokal and Rohlf, 1969) reveal a highly significant variation among the 20 populations ($P \leq .001$), and a non-significant variation among individual plants within a population. The samples clearly fall into two

groups. Card Pond, Prospect Lake, Broad Brook, and Lake Buel form one group; their mean leaf widths are all greater than 2.5 mm, and their ranges do not extend below 2 mm. On this basis, these four should be classified as *E. canadensis* (see Table 1). Flowers characteristic of *E. canadensis* were produced by plants of the Broad Brook population in culture. None of the areas where these four populations were collected exhibited such overt signs of pollution as high turbidity, foul odor, oil scum, or algal bloom.

TABLE 3

Collection site, location by town, and mean, 95% confidence interval and range of leaf width for 20 populations of *Elodea* collected in western Massachusetts.

Collection Site	Location by Town	Mean and Confidence Interval	Range
Prospect Lake	Egremont	3.31 ± 0.18	2.50-4.00
Card Pond	West Stockbridge	3.19 ± 0.25	2.25-4.75
Lake Buel	Monterrey	2.99 ± 0.14	2.00-4.00
Broad Brook	Easthampton	2.62 ± 0.18	2.00-4.00
Harts Brook	Hadley	1.75 ± 0.13	1.50-2.25
Chapin Pond	Ludlow	1.67 ± 0.06	1.25-2.00
Benton Pond	Otis	1.63 ± 0.08	1.25-2.00
Lake Garfield	Monterrey	1.54 ± 0.18	1.00-2.50
Ashley Pond	Holyoke	1.44 ± 0.08	1.25-2.00
Porter Lake	Springfield	1.43 ± 0.06	1.00-1.75
Congamond Lake	Southwick	1.42 ± 0.09	1.00-2.00
Hulbert's Pond	Northampton	1.34 ± 0.11	1.00-1.75
Pequot Pond	Westfield	1.29 ± 0.05	1.00-1.75
Center Pond	Becket	1.25 ± 0.13	1.00-2.00
Manhan River	Southampton	1.23 ± 0.07	1.00-1.50
Paradise Pond	Northampton	1.22 ± 0.06	1.00-1.50
Nashawannuck Pond	Easthampton	1.20 ± 0.08	1.00-1.75
Forge Pond	Granby	1.18 ± 0.05	1.00-1.50
Buck Pond	Westfield	1.11 ± 0.04	1.00-1.50
Norwich Pond	Huntington	1.03 ± 0.03	1.00-1.50

Twelve of the sample populations have mean leaf widths of less than 1.5 mm: Hulbert's Pond, Forge Pond, Ashley Pond, Porter Lake, Congamond Lake, Buck Pond, Center Pond, Pequot Pond, Manhan River, Nashawannuck Pond, Paradise Pond, and Norwich Pond. Flowers typical of *Elodea nuttallii* were observed in the Hulbert's Pond, Nashawannuck Pond, and Paradise Pond populations. On the basis of their leaf widths, these are apparently *E. nuttallii*. Several of these 12 populations of *E. nuttallii*, including Hulbert's Pond and Nashawannuck Pond have ranges extending beyond the 1.5 mm limit, and three exceed the 1.8 mm limit set by some authorities.

Four populations remain unclassifiable: Chapin Pond, with mean leaf width 1.67 mm; Lake Garfield, 1.54 mm; Benton Pond, 1.63 mm; and Harts Brook, 1.75 mm. Flowering was not observed in any of these populations. It is conceivable that flowers are not as definitive a taxonomic criterion as is supposed, most herbarium specimens being based on strictly vegetative material (Radford et al., 1964), and *Elodea canadensis* and *E. nuttallii* may not be as clearly differentiated as presumed. Fertile crosses of *E. canadensis* with *E. nuttallii* have been reported (Ernst-Schwarzenbach, 1945), and these unclassifiable populations may be of hybrid origin. These four populations could represent another previously undescribed species or one of the other species of limited distribution outside its known range. They may also be specimens of *E. canadensis* with decreased leaf width as a response to environmental conditions. Chromosome counts will not aid in species identification, because diploid numbers overlap and seem to vary (Radford et al., 1964; Darlington and Ammal, 1945; Santos, 1924).

SUMMARY

Elodea canadensis and *E. nuttallii* are economically important plants because of their occurrence as troublesome waterweeds and their potential use as indicators of pollution. Due to infrequent and brief flowering, leaf morphol-

ogy is often used to differentiate species. In an experimen designed to test the effects of elevated temperature on th vgetative morphology of *E. canadensis*, leaf width wa reduced, and leaves were produced which fell within th reported range of *E. nuttallii*. Accepted taxonomic criteri for distinguishing *E. canadensis* and *E. nuttallii* were no upheld in four of 20 populations sampled in western Mas sachusetts.

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